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# Doubly nonlocal reaction-diffusion equations and the emergence of species

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#### ABSTRACT

The paper is devoted to a reaction-diffusion equation with doubly nonlocal nonlinearity arising in various applications in population dynamics. One of the integral terms corresponds to the nonlocal consumption of resources while another one describes reproduction with different phenotypes. Linear stability analysis of the homogeneous in space stationary solution is carried out. Existence of traveling waves is proved in the case of narrow kernels of the integrals. Periodic traveling waves are observed in numerical simulations. Existence of stationary solutions in the form of pulses is shown, and transition from periodic waves to pulses is studied. In the applications to the speciation theory, the results of this work signify that new species can emerge only if they do not have common offsprings. Thus, it is shown how Darwin's definition of species as groups of morphologically similar individuals is related to Mayr's definition as groups of individuals that can breed only among themselves.

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#### 1. Nonlocal equations in population dynamics

Nonlocal reaction-diffusion equations arise in various applications. In population dynamics they are widely used in order to describe nonlocal consumption of resources [1–3] or breeding with different phenotypes [4–6]. The roles of these nonlocal terms are quite different, from the biological and from the modeling points of view. In this work, we will consider both of them at the same time and will study their mutual influence. Their combination will allow us to make some important conclusions about the emergence of biological species.

We consider the nonlocal reaction-diffusion equation

$$\frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2} + a(S(u))^2 (1 - J(u)) - bu, \tag{1.1}$$

where *D*, *a* and *b* are some positive constants

$$S(u) = \frac{1}{2h_1} \int_{-\infty}^{\infty} \psi(x - y)u(y, t)dy, \quad \psi(z) = \begin{cases} 1, & |z| \le h_1, \\ 0, & |z| > h_1 \end{cases}$$

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$$J(u) = r(h_2) \int_{-\infty}^{\infty} \phi(x - y) u(y, t) dy, \quad \phi(z) = \begin{cases} 1, & |z| \le h_2 \\ 0, & |z| > h_2 \end{cases}$$

We take the kernels of the integrals in the form of step-wise constant functions in order to simplify analysis and simulations. Other kernels can also be considered. We consider two forms for  $r(h_2)$ , depending on whether  $h_2$  is small or large. In case of small  $h_2$ , we set  $r(h_2) = 1/(2h_2)$  so that for  $h_2 \rightarrow 0^+$  we find J(u) = u, similar to the local consumption of resources in the logistic equation. In the case of asymptotically large  $h_2$  we set  $r(h_2) = 1$ . Then in the limit of large  $h_2$  we obtain global consumption of resources with the integral  $I(u) = \int_{-\infty}^{\infty} u(y, t) dy$  in the consumption term.

In this work, we will study traveling waves described by Eq. (1.1), periodic traveling waves, stationary and moving pulses. Let us recall that traveling wave is a solution u(x, t) = w(x - ct) of this equation which propagates with a constant speed c. For the periodic traveling wave, its speed of propagation and its profile change periodically in time. By stationary pulses we understand stationary solutions of this equation with zero limits at infinity, and by moving pulses nonstationary spike solutions.

Various particular cases of Eq. (1.1) are studied in the literature (see [3,7] and the references therein). In the limit of small  $h_1$  and  $h_2$  we obtain the reaction-diffusion equation for single species population growth,

$$\frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2} + a u^2 (1 - u) - b u, \tag{1.2}$$

where the second power of the population density corresponds to sexual reproduction [8]. If b < a/4, then the equation  $au^2(1-u) - bu = 0$  has three zeros,  $u_+ = 0$ ,  $u_0 = (1 - \sqrt{1 - 4b/a})/2$  and  $u_- = (1 + \sqrt{1 - 4b/a})/2$ . In this case, there is a traveling wave solution of this equation, u(x, t) = w(x - ct) with the limits  $w(\pm \infty) = u_{\pm}$ . It exists for a unique value of *c* and it is globally asymptotically stable (see [3] and the references therein). This equation also has stationary solutions in the form of pulses, that is positive solutions with zero limits at infinity. Such solutions are unstable.

If  $h_1 > 0$  and  $h_2 = 0$ , then Eq. (1.1) corresponds to the local consumption of resources and breeding with possibly different phenotypes (see Appendix):

$$\frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2} + a(S(u))^2 (1-u) - bu.$$
(1.3)

Similar to the previous case, existence and stability of traveling waves for this equation is proved [4–6]. The next particular case of Eq. (1.1) is  $h_1 = 0$  and  $h_2 > 0$ :

$$\frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2} + a u^2 (1 - J(u)) - b u.$$
(1.4)

Contrary to the previous equation, the maximum principle is not applicable here, and the existence of wave is proved only for  $h_2$  sufficiently small [9] or in some other special cases [10]. Propagation of periodic traveling waves is observed in numerical simulations for the values of  $h_2$  greater than some critical value  $h_2^*$  for which the homogeneous in space solution  $u = u_-$  loses its stability resulting in appearance of stationary periodic solutions.

In the monostable case ( $u^2$  in the production term is replaced by u), existence of waves is proved for all speeds greater than or equal to the minimal speed [11–14], stability of waves is studied in [15], their dynamics in [9,16–19]. Systems of equations are studied in [3,20,21].

Eq. (1.4) has stationary solutions in the form of pulses for all  $h_2$  sufficiently large  $(r(h_2) = 1)$  [22]. Numerical simulations show that these pulses are stable [23–25], though their stability is not proved analytically.

Thus, Eq. (1.4) has traveling waves propagating with a constant speed and profile for  $h_2$  sufficiently small. Periodic waves are observed for intermediate values of  $h_2$  and pulses for  $h_2$  sufficiently large. Transition from periodic waves to pulses occurs through a global bifurcation where the speed of the periodic wave converges to zero and the peaks of the wave form the pulses [25].

Eq. (1.4) is a limiting case of Eq. (1.1) as  $h_1$  converges to 0. In this work, we will study how the dynamics of the solution are influenced by the integral S(u) for positive  $h_1$ . The linear stability analysis of the homogeneous in space solutions is presented in Section 2. Dynamics of pulses and waves is discussed in Section 3. The derivation of the model and positiveness of solutions are discussed in the Appendix.

One of the important applications of nonlocal reaction–diffusion equations concerns the theory of speciation. Nonlocal consumption of resources allows the description of the emergence of biological species [26,27]. The integral S(u) in the reproduction term is determined by the relation between the phenotypes of parents. We will show that speciation can occur only if this distribution is sufficiently narrow. This is related to Mayr's definition of species as a group of individuals that can breed only among themselves. We discuss these questions in Section 4.

#### 2. Linear stability analysis

#### 2.1. Nonlocal consumption

We begin with the stability analysis of a stationary solution homogeneous in space. Linearizing Eq. (1.1) about  $u = u_* (= u_{\pm}, u_0)$ , we obtain the eigenvalue problem

$$Dv'' + 2au_*(1 - u_*)S(v) - au_*^2J(v) - bv = \lambda v.$$

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